

ANATOMY OF *DIASTOMA MELANOIODES* (REEVE,
1849) WITH REMARKS ON THE SYSTEMATIC
POSITION OF THE FAMILY DIASTOMATIDAE
(PROSOBRANCHIA: GASTROPODA)

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Abstract.—*Diastoma melanioides* is the living survivor of a long lineage of snails in the Family Diastomatidae that occurred in the Tethys Sea during the Tertiary. Study of the anatomy shows that this species has open pallial gonoducts, and aphyallic males, which establishes it in the superfamily Cerithiacea. A large ovipositor on the right side of the foot extends into the mesopodium. The radula is taenioglossate; the alimentary tract has paired salivary glands that run through the nerve ring and a stomach with style sac, gastric shield and reduced spiral caecum. The cephalic cavity is large and accommodates a small buccal mass and lengthy buccal and labial nerves. The nervous system is moderately condensed. Living animals occur subtidally in shallow water where they burrow in sandy bottoms and graze on algae and detritus. Development appears to be direct. *Diastoma melanioides* most closely resembles members of the Cerithiidae in anatomy and ecology. Anatomical and shell characters, and the fossil record indicate that *Diastoma* should be given familial status. The family is placed close to the Cerithiidae, the Potamididae, and the freshwater Melanopsidae.

Introduction

Diastoma melanioides (Reeve) is a relatively unknown cerithiacean prosobranch of moderate size which is restricted to a limited area of the coastline of the Great Australian Bight. It is the sole survivor of the *Diastoma* lineage, Family Diastomatidae. The taxonomic limits of this family have been poorly defined; consequently, a number of heterogeneous groups have been referred to the Diastomatidae by numerous authors, and the family has been expanded well beyond the original concept. The living relict, *Diastoma melanioides*, heretofore known only from its shell, is rare in most museum collections and unfigured in most publications. Recently, some well-preserved specimens collected at Esperance, Western Australia, were sent to me through the kindness of Mr. Alan Longbottom. This material has provided information about the operculum, radula, and anatomy of *Diastoma melanioides* which unequivocally establishes that it is a cerithiacean.

The account that follows presents a description of the shell and internal

anatomy, reviews the literature, and sets definite systematic limits to the family by providing familial and generic descriptions and a synonymy.

Material and Methods

Fourteen specimens of *Diastoma melanioides* were sent to me for examination by Mr. Alan Longbottom of Esperance, Western Australia. Eight of these were well-preserved animals and were dissected under a Wild M-5 stereo dissecting microscope. A one percent Methylene Blue aqueous solution was used as a stain. Protoconchs, shell ultrastructure, radula and periostracum were studied with a Nova-Scan SEM. All measurements are relative to average-sized snails (see Table 1). There was not sufficient material for statistical measurements of the soft parts.

Although anatomical observations are substantially accurate, the limited material and its preserved state may not have shown all the details of the fragile pallial gonoduct, stomach and smaller nerves. My work should be reconfirmed by the study of living snails.

Description

List of abbreviations.—*a*—anus; *bg*—buccal ganglion; *bm*—buccal mass; *bt*—buccal tensor; *cbc*—cerebral-buccal connective; *cc*—cerebral cavity; *cg*—cerebral ganglion; *cme*—cut mantle edge; *ct*—ctenidium; *d*—dialyneury; *dg*—digestive gland; *dln*—dorsal labial nerve; *es*—esophagus; *exh*—exhalant siphon; *f*—foot; *ff*—fold emerging from spiral calcum; *ga*—glandular area; *gs*—gastric shield; *hg*—hypobranchial gland; *i*—intestine; *il*—inner lamina; *inh*—inhalant siphon; *j*—jaws; *k*—kidney; *lln*—lateral labial nerve; *lmn*—left mantle nerve; *lpg*—left pleural ganglion; *lsg*—left salivary gland; *m*—mouth; *mn*—mantle nerve; *mp*—mantle papillae; *mpg*—mesopodial ganglion; *ng*—nerve ganglion; *nr*—nerve ring; *od*—oviduct; *odd*—opening of digestive diverticula; *og*—oviducal groove; *ol*—outer lamina; *on*—optic nerve; *op*—operculum; *ovp*—ovipositor; *os*—osphradium; *osd*—opening of salivary duct; *ov*—ovary; *pes*—posterior esophagus; *pg*—pedal ganglion; *pod*—proximal end of pallial oviduct; *ppg*—propodial groove; *psg*—proximal end of salivary gland; *r*—rectum; *rd*—radula; *rcg*—right cerebral ganglion; *rpg*—right pleural ganglion; *rsg*—right salivary gland; *sa*—sorting area; *sbg*—subesophageal ganglion; *sbn*—subvisceral nerve; *sbv*—subvisceral connective; *sc*—spiral caecum; *sd*—sperm duct; *sec*—supraesophageal connective; *sg*—salivary gland; *sn*—snout; *spg*—supraesophageal ganglion; *sp*—spermatophore receptacle; *sr*—seminal receptacle; *ss*—style sac; *st*—stomach; *t1*—typhlosole 1; *t2*—typhlosole 2; *tn*—tentacle nerve; *wcc*—wall of cerebral cavity.

Specimens examined.—Abbreviations: AMS = Australian Museum,

Sydney; USNM = United States National Museum; WAM = Western Australian Museum.

Western Australia: Cheyne Beach, 40 mi E of Albany, 34°47'S, 118°25'E (AMS); Cheyne Beach, near Posidonia, 34°47'S, 118°25'E (WAM); Cape Riche, 70 mi E of Albany, 34°37'S, 118°46'E (AMS); North Side of High Island, Duke of Orleans Bay, 33°55'S, 122°37'E (WAM); Esperance Bay, Esperance (USNM, 806583, 801614); Mississippi Bay, 30 mi E of Esperance, 34°00'S, 122°17'E (AMS); Eyre Highway, 65 mi E of Madura, 31°55'S, 127°00'E (AMS).

South Australia: Port Sinclair, 32°06'S, 133°00'E (AMS); Smokey Bay, 32°20'S, 133°47'E (AMS); Streaky Bay, 32°32'S, 134°08'E (AMS).

Shell (Table 1; Fig. 1A–D, G–J).—Shell elongate, length 30–50 mm, turreted, having apical angle of 25 degrees and comprising 10–13 convex whorls. Protoconch (Fig. 1I) has two convex, smooth whorls. Transition from protoconch to teleoconch sharply defined by straight lip of protoconch and sudden change in sculpture. First two whorls of teleoconch sculptured with 3 weak spiral cords which increase to 4 on the third whorl. Spiral cords weak, increasing in number but diminishing in intensity on each successive whorl. Slanting axial ribs appear on fourth teleoconch whorl and are most pronounced and numerous (12–18) on median whorls of shell but become weaker and nearly lost on penultimate and body whorls. Overall fine cancellate sculpture results from intersection of axial ribs and spiral cords. Varices occasionally present as low flat axial ridges. Suture straight, deeply incised, forming ramp at posterior of each whorl that becomes most pronounced on body whorl where outer lip of aperture is slightly detached from body whorl to form anterior apertural notch. Aperture (Fig. 1H) tear-shaped, wide at base and a little over one-third the length of shell. Anterior siphonal canal virtually absent but distinguishable as shallow, depressed curve of apertural basal lip. No anal canal present. Columella slightly convex with slight but distinct median oblique fold originating from base of outer apertural lip and continuing into aperture of the shell where it ends about halfway up body whorl. Slight columellar callus present. Outer lip of aperture continuous, not broken by anterior canal, thin, smooth and slightly curved. Shell color white, flecked with small, spirally arranged, light brown spots and blotches. Largest blotches at posterior of each whorl, adjacent to suture.

Periostracum (Fig. 3D–F) thin and tan colored, covering entire shell and with spiral rows of tiny hair-like projections that correspond to underlying spiral sculpture of shell. Periostracum on live collected specimens has overall fuzzy appearance but flakes off easily when dry.

Operculum (Fig. 1J, K) dark brown, ovate and paucispiral with nucleus near the columellar edge. Operculum closes aperture when animal withdrawn.



Fig. 1. A–D. Dorsal, ventral and side views of the shell of *Diastoma melanioides* (49.7 mm long). Shell in A has been whitened with Ammonium chloride to enhance shell sculpture; E–F, Shells of the Eocene fossil *Diastoma costellata*, from the Paris Basin. Note the pronounced sutural ramp at aperture. (52 mm long). G–H. Shell apex (G), and adult whorls and aperture (H) of *Diastoma melanioides* showing details of shell sculpture; I, SEM micrograph of protoconch of *Diastoma melanioides* showing change from embryonic to juvenile shell sculpture; J–K. Operculum showing free surface (J) and attached side with muscle scar (K).

Animal: external features (Fig. 2A, B, D).—Base color white to flesh with a few tiny flecks of brownish pigment on head-snout. Head with a large, highly extensible, spade-shaped snout (*sn*) deeply incised with transverse wrinkles. Cephalic tentacles short, about one-third the length of snout, and widening to a peduncle where attached to head. A tiny black eye present

Table 1.—Analysis of shell characters of *Diastoma melanioides*. (Measurements in mm.)

Character (n = 10)	\bar{x}	SD	Range
Length	38.58	5.93	30–49.68
Width	11.73	1.34	9.48–14.08
No. of whorls	11.7	0.95	10–13
No. axial ribs per whorl	16.1	1.97	12–18
Aperture length	11.06	1.28	9.25–13.44
Aperture width	4.87	0.45	4.20–5.82

on outer edge of each peduncular stalk. The relatively large foot (*f*) has a propodial grove (*ppg*) (anterior pedal mucous gland). A furrow emerges from the exhalant siphon and runs down the right side of the foot. In females, a large, bulbous, vermiform ovipositor emerging from a deep pit is present on the median right side of the foot (Fig. 2B, C). Mantle edge thick, characterized by a sharply defined ridge at the exhalant siphon (*exh*). Upper margin of mantle edge bifurcate, with thin, membranous fringe from which emerges another papillated fringe (*mp*). Mantle papillae are short and fused with each other at their bases. Inhalant siphon (*inh*) marked by a thickening of mantle wall and by papillae wider than those at dorsal mantle edge. No papillae on ventral edge of mantle. Mantle thin, unpigmented, forming dorsal fold that begins at exhalant siphon and extends back for one-half of the first whorl. Major mantle organs visible through mantle wall. Tan colored, single-lobed kidney (*k*) of moderate size present. Digestive gland (*dg*) dark brown. Gonads occupy dorsal parts of upper whorls.

Mantle cavity and associated organs (Fig. 2D).—The deep, spacious mantle cavity occupies the last two whorls of the animal. A thick glandular area (*ga*) lies on the inner side of the mantle edge adjacent to the tip of the inhalant siphon. The bipectinate osphradium (*os*) is a thin brown ridge comprising about 140 thick filaments and is about 13.5 mm long and 0.2 mm wide. It lies adjacent to the ctenidium but is separated from it by a narrow margin of thin mantle tissue. The osphradium curves away from the ctenidium at its distal end and twists toward the inhalant siphon. The monopectinate ctenidium (*ct*) is large, about 17 mm long, 2.3 mm wide, and comprises 195 thin leaflets. A long, wide hypobranchial gland (*hg*) lies adjacent to the ctenidium and excretes much mucus. It is composed of thick transverse folds which become darker and wider at the distal end, adjacent to the anus and exhalant siphon. The osphradium, ctenidium and hypobranchial glands do not extend the length of the mantle cavity but end about a third of the way from its proximal end. The rectum (*r*) is filled with ovoid fecal pellets comprised of sand grains, detritus, and algal fragments. The pallial gonoducts extend the length of the mantle cavity, and are open in both sexes. The

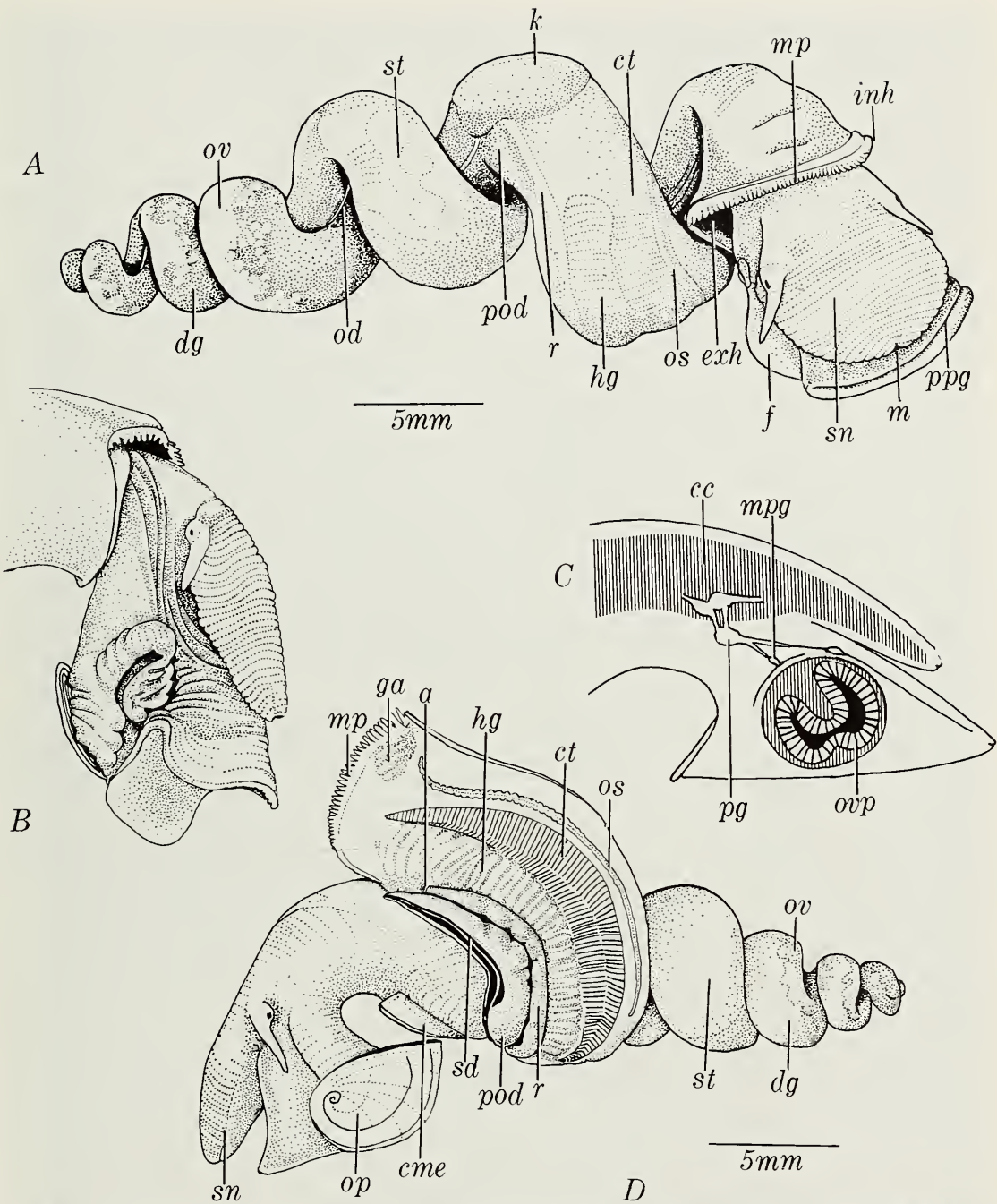


Fig. 2. A, *Diastoma melanioides*, female removed from shell and viewed from right dorsal side; B, Female showing large bulbous ovipositor on right side of foot and ciliated groove leading to it from exhalant siphon; C, Midsagittal section through head-foot showing interior of ovipositor with mucus gland, central cavity and innervation by nervous system; D, Female removed from shell, mantle cavity opened along left side and mantle folded to right.

spacious proximal mantle cavity contains a large pericardial sac that accommodates a large auricle and ventricle. The single-lobed kidney (Fig. 2A, *k*) has a large slit-like opening on its ventral surface that leads into the mantle cavity.

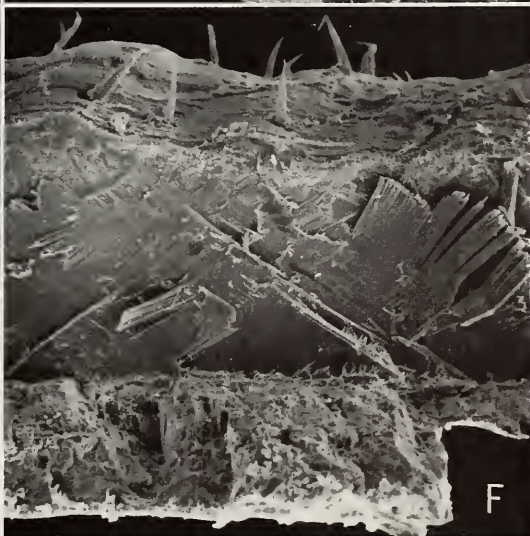
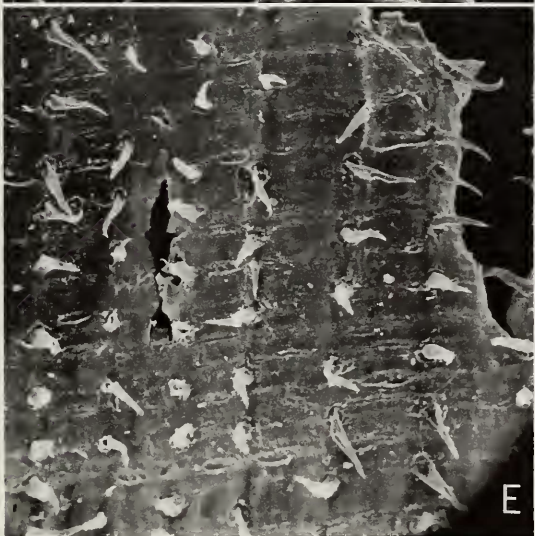
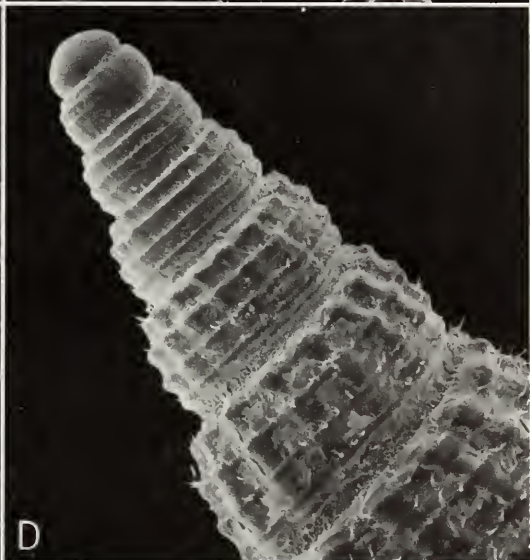
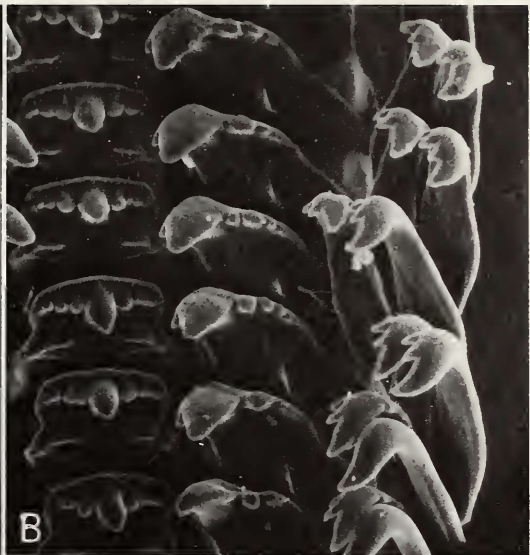
Alimentary system (Fig. 4).—*Diastoma* has a spacious cephalic cavity (hemocoel). The highly extensible snout is dominated by bundles of circular muscle. The mouth (*m*) is deeply recessed between the two lobes of the snout apex. The jaws (*j*) are thin and brittle, each about 1.3 mm long. Under the microscope, they appear scale-like near their cutting edges. The radular ribbon (Fig. 3A–C) is tiny, about 3.8 mm long, 0.6 mm wide and comprising 50 rows of teeth. It is about one-eleventh the length of the shell and is typically taenioglossate (2 + 1 + 1 + 1 + 2), not unlike those of some *Cerithium* species. Rachidian tooth quadrate in shape, concave laterally and convex basally. Cutting edge of rachidian has spade-shaped, pointed, central cusp flanked on each side with 2–4 smaller blunt denticles. Basal plate of rachidian tooth has pair of basolateral projections. Lateral tooth rhomboidal in shape, laterally elongate where it is attached onto the basal radular membrane. Top of lateral tooth has cutting edge with tiny inner denticle, a large, triangular, pointed cusp and 2–3 tiny denticles, respectively. Base of lateral tooth straight. Basal plate with centrally located, small, blunt peg. Marginal teeth long, slender, swollen centrally, curving and with spatulate tips. Cutting edge of inner marginal tooth has 2 sharp inner denticles, a long, pointed, central cusp and a short blunt outer denticle. Outer marginal tooth identical but lacks outer denticle.

The buccal mass (*bm*) is relatively small, about 3 mm long, and is attached anteriorly to the inner tip of the cephalic cavity by numerous, thin muscular tensors (*bt*). Originating at the center of the ventral buccal mass is a long, post-median retractor muscle that inserts on the ventral wall of the cephalic cavity. It is flanked by 2 smaller retractors. The radula sac originates at the central posterior part of the buccal mass and extends dorsally.

The esophagus (*es*) is long, narrow and loosely connected to the base and sides of the buccal body cavity by several long, thin muscles. The largest of these extend from the esophagus to the nerve ring and then to the walls of the cephalic cavity (*m*). The esophagus may thus be partially pulled through the nerve ring when the snout is extended. Attached to the dorsal surface of the anterior esophagus are a pair of long tubular, convoluted salivary glands (*sg*) which pass through the nerve ring and end on the mid-esophagus, where they are twisted to its left side (Fig. 5D). Each salivary gland empties into a side of the median buccal cavity (Fig. 4, *osd*). The

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Fig. 3. SEM micrographs: A, Radula of *Diastoma melanioides* showing unworn portion of radular ribbon (0.6 mm wide); B, Details of rachidian, lateral and marginal teeth (0.3 mm wide); C, Close up of lateral tooth (0.15 mm long) showing its insertion on basal radular membrane; D, SEM micrograph of protoconch and juvenile whorls of shell to show early sculpture and periostracum (15×); E, SEM of periostracum illustrating microscopic periostracal hairs (50×); F, Cross section of shell showing periostracum at top and lamellar aragonite below (50×).



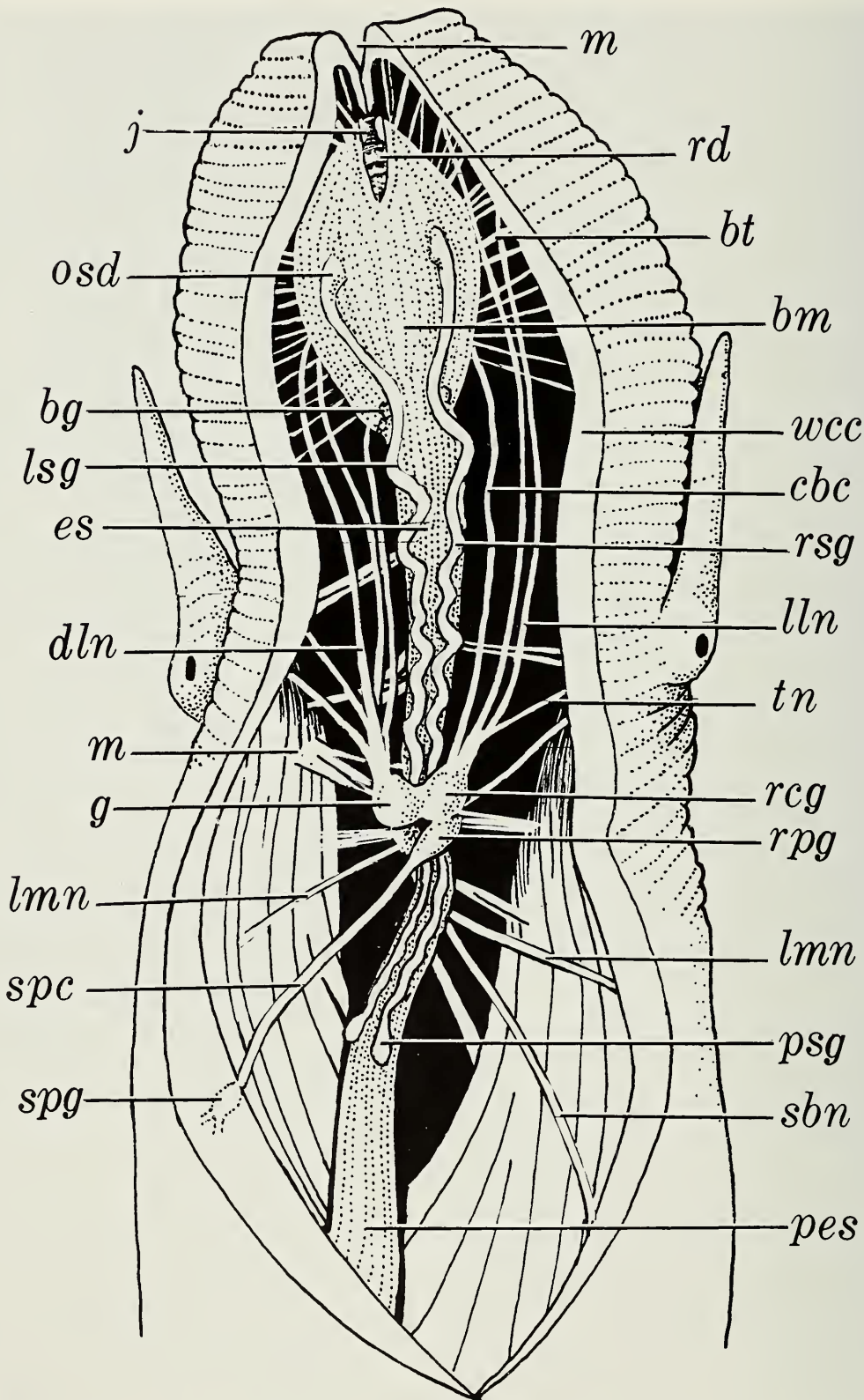


Fig. 4. Dissection of head of *Diastoma melanioides* opened by a dorsal longitudinal cut to expose cephalic cavity and anterior alimentary tract (buccal mass 3 mm long).

anterior esophagus has a dorsal food groove and two dorsal ridges (Fig. 5E) which become ventral-lateral (Fig. 5F) as they pass through the nerve ring. The mid-esophagus is flattened dorso-ventrally and the dorsal food ridges become more laterally placed.

The stomach (Fig. 5G) is typically cerithiacean and is a large organ almost one and a half whorls in length. It has a well-defined sorting area (*sa*) comprised of transverse lamellae-like folds, a style sac (*ss*), a large cuticular gastric shield (*gs*) and 2 liver ducts (*odd*). Posterior to the gastric shield is a large pad-like area (*ff*) of uncertain function which arises from the reduced spiral caecum (*sc*). No crystalline style was found but this was probably due to the preserved state of the animals.

Reproductive system (Fig. 5A).—The presence of open pallial gonoducts, aphyallic males, spermatophores, and the location of the seminal receptacle are typically cerithiacean. Males are smaller than females and easily distinguished from them by the lack of an ovipositor on the right side of the foot. The narrow laminae of the pallial gonoducts are thin walled and glandular at the proximal end of the gonoduct where the outer lamina becomes thickened and white along its base. This area is probably the prostate and spermatophore-forming organ. The white testis overlays the digestive gland on the dorsal surface of each upper whorl.

The long pallial gonoduct of females is a larger, wider organ than in males (Figs. 2D, 5A). The deep slit-like oviducal groove (*og*) formed by the 2 laminae of the open duct is lined with numerous transverse folds of glandular tissue which become thick and more opaque at the proximal end of the duct. This is the albumen gland (*ag*). The pallial oviduct ends just anterior to the anus. A narrow slit, the sperm-collecting gutter (*sd*), lies along the free edge of the outer lamina (*ol*) enlarging to form a pouch-like seminal receptacle (*sr*) which is located in the post-median section of the lamina. The seminal receptacle is a flattened, kidney-shaped structure with a spongy interior that initially receives the spermatophore and also serves to hold the sperm. A central axial flap of tissue divides it into 2 chambers that join at the end. I extracted the remains of what appeared to be a disintegrating spermatophore from the inner chamber. The seminal receptacle is narrow at its proximal end and becomes a blind tube (*sr*) in the proximal part (*pod*) of the outer lamina of the oviduct. No opening from the receptacle to the oviducal groove was found.

The ovary (Fig. 2A, *ov*) lies on the dorsal surface of the digestive gland (*dg*) and is light tan. Oocytes are about 0.4 mm in diameter and are shaped like rounded triangles.

One of the most unusual structures associated with the female reproductive tract of *Diastoma* is the large ovipositor (Fig. 2B, C) on the right median part of the mesopodium. This ball-like pad has a crescent-spiral configuration that sinks into a deep pit at its center (Fig. 2C, *ovp*). The pit leads into

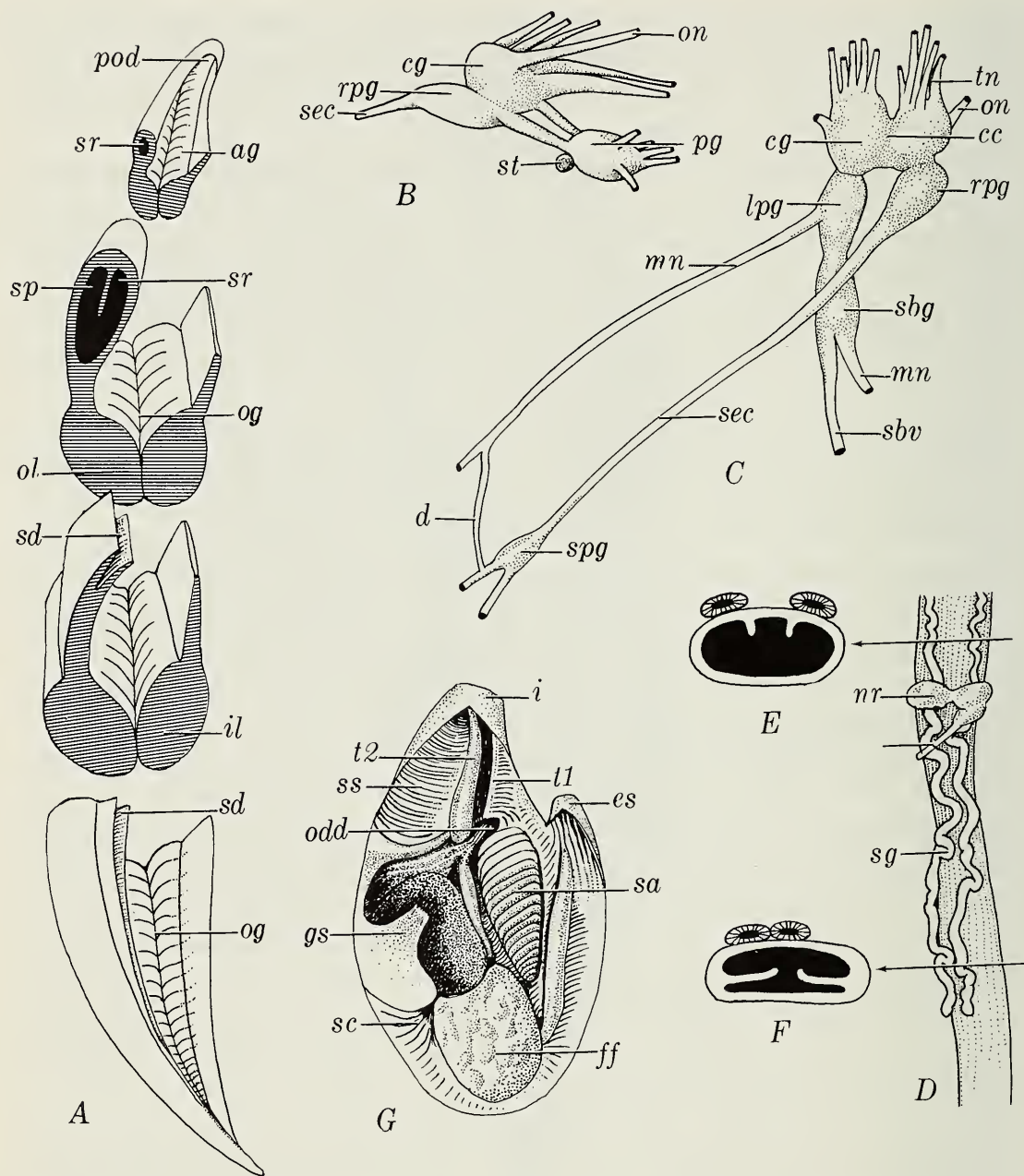


Fig. 5. A, Diagrammatic representation of pallial oviduct with sections of duct cut away to show arrangement of laminae and associated ducts, spermatophore and seminal receptacles. Pallial oviduct is 10 mm long and oriented with distal end at bottom of figure; B, Lateral view of cerebropedal complex; C, Dorsal view of nerve ring and associated nerves; D, Anterior and mid-esophagus with nerve ring and salivary glands; E, Section through anterior esophagus showing dorsal folds and salivary ducts; F, Section through mid-esophagus showing ventral-lateral (dorsal) folds and salivary ducts; G, Stomach opened with a mid-dorsal longitudinal cut to expose inner anatomy.

a large cavity in the center of the foot. The cavity is lined with thick glandular tissue embedded in the muscular mesopodium and is connected with the pedal hemocoel. The organ and cavity taper toward the left side of the foot. The ovipositor is innervated by a pair of nerves originating from the metapodial ganglia (*pg*). Although the exact function of the ovipositor was not observed, it is undoubtedly associated with the formation of the jelly egg mass. In preserved specimens the cavity is filled with a viscous mucus and continues to emit mucus when placed in water. There is no evidence that it is a brood sac.

Nervous system (Fig. 4, 5B, C).—*Diastoma* has an epiathroid nervous system that is moderately condensed with a layout typical of cerithiaceans. The RPG ratio of Davis et al. (1976:263) (length of the pleurosupra-esophageal connective divided by the sum of the lengths of the supraesophageal ganglion, pleuro-supraesophageal connective and right pleural ganglion) is 0.69, a median value between those observed in members of the Cerithiidae and the Potamididae. The most characteristic features of the nervous system are the long labial (Fig. 4, *lln*, *dln*) and proboscis nerves which emerge from the cerebral ganglia (*rcg*, *lcg*). These lie free within the cephalic cavity in a "loose" state and are surrounded with little connective or muscular tissue. The large cerebral ganglia (Fig. 5B, C, *cg*) are almost fused to each other. Each of the pleural ganglia (*rpg*, *lpg*) are joined to the cerebral ganglia with short thick connectives. The right pleural ganglion (*rpg*) gives rise to a long supraesophageal connective (*sec*) that ends in the supraesophageal ganglion (*spg*) which is embedded in the left body wall. This ganglion emits a nerve that is connected to the left mantle nerve by a long dialyneury (*d*). The left pleural ganglion (*lpg*) is joined to the subesophageal ganglion by a short thick connective. A long visceral nerve (*sbv*) and a typical visceral loop are present. The 2 pedal ganglia (*pg*) are joined to the cerebral and pleural by moderately short, slender connectives. The pedal commissure is short and thick. A large statocyst (*st*) containing numerous statoliths lies at the posterior base of each pedal ganglion. Two long major connectives run from each pedal ganglion to the propodial and mesopodial ganglia (Fig. 2C, *mpg*). The mesopodial ganglia give rise to the nerves that innervate the ovipositor. All ganglia are pink in color.

Systematics

Diastomidae Cossmann, 1894:322; 1906:173–174.—Wenz, 1940:749–750.—Pchelintsev and Korobkov, 1960:159.—Franc (*in* Grassé) 1968:281.—Gründel, 1976:71–75.—Ladd, 1972:27.—Wilson and Gillett, 1979:61.—Rehder, 1980:33 (*non* Diastomidae Cossmann).

Diastomatidae (emend. *pro* Diastomidae) Ludbrook, 1971:31; 1978:112.

This family comprises many fossil species and one Recent one. It is characterized by individuals having turreted, elongate shells with convex whorls

and ovate apertures with continuous outer lips and wide shallow anterior canals. Former varices are normally present. A paucispiral operculum, taenioglossate radula, paired salivary glands, stomach with style sac and gastric shield, a deep mantle cavity with open pallial gonoducts, and the absence of a penis are characteristic of the living animal.

Remarks.—The family, as originally proposed by Cossmann (1894:322–323), included a group of fossil genera (*Sandbergeria* Bosquet, *Cryptaulax* Tate, *Exelissa* Piette, *Teliostoma* Harris and Burrows, *Aurelianelle* Cossmann) centered around the genus *Diastoma* Deshayes. Cossmann (1906:173) subsequently treated the family in more detail and added the genera (subgenera) *Aneurychilus* Cossmann and *Cerithidium* Monterosato. With the exception of *Cerithidium* and *Diastoma*, all of these taxa represent fossil groups. Cossmann appears to have been unaware that *Diastoma* is still extant in southern Australia, represented by *Diastoma melanioides* Reeve. This is probably due to the fact that Reeve (1849) originally placed it in *Mesalia*, a turritellid genus.

The original concept of the family is somewhat heterogeneous, exemplified by Cossmann's (1906:174) division of the family into "cerithid," "rissoid" and "bacilliform" groups. The subsequent expansion of the family by the inclusion of various other small-shelled groups has distorted the family concept into an unnatural polyphyletic group. This is reflected in the literature and has been recently acknowledged by Ludbrook (1971) and Gründel (1976). A brief summary of the history of the family concept follows.

Initially, the family was expanded to include other genera of small-shelled mesogastropods by Dall (1889:258), who, misled by Deshayes' (1861:413) statement of an affinity between *Diastoma* and the rissoids, also suggested that *Diastoma* was related to *Alaba* and a *Bittium* species. It is likely that Dall had never seen the fossil *Diastoma* species from the Paris Basin and merely compared the figures of them with *Alaba* and the common southeastern Atlantic species, *Bittium varium* Pfeiffer. He was also unaware of the existence of the living relict, *Diastoma melanioides*. Dall's (1889) assignment of *Bittium varium* to *Diastoma* probably led other workers such as Bartsch (1911), Wenz (1940) and Franc (1968) to equate cerithiacean species of the genera *Finella*, *Alaba*, and *Alabina*, all having small shells with shallow anterior canals which superficially resemble those of the large fossil *Diastoma* species, with the Diastomatidae. Both Wenz (1940) and Franc (1968) synonymized the Finellidae and the Alabinidae with the Diastomatidae. Neither worker was aware that a living species of *Diastoma* existed. This led more recent authors such as Ladd (1972:27), Kensley (1973:281), and Abbott (1974:107) incorrectly to assign other small-shelled cerithiacean snails of the genera *Bittium*, *Alabina*, *Obtortio*, and *Diala* to the Diastomatidae.

Tate (1894:176–177), Finlay and Marwich (1937:42), Marwick (1957:163), and Ludbrook (1971) were the only authors to point out that *Diastoma* has a living representative. Ludbrook (1971) also noted that many of the small cerithiids referred to *Diastoma* should be excluded from that group. Her treatment of the family, although brief, is substantially in agreement with my findings.

Gründel (1976) suggested that the Diastomatidae was a primitive group which arose in the Triassic and gave rise to the Cerithiacea. He believed that the Cerithiidae split off from the Diastomatidae in the Cretaceous and that *Diastoma* was a short-lived unsuccessful side branch of mainstream cerithiacean evolution. Within his classificatory scheme, Gründel (1976:75) divided the Diastomatidae into two subfamilies, the Diastominae, which included the Bittiinae and Diastomiinae, and the Finellinae to which he assigned the tribes Finellini and Scaliolini. Thus he included within the subfamily Finellinae genera such as *Sandbergeria*, *Eufinella*, *Obtortio*, *Fesandella*, and *Scaliola*. Gründel did not cite Ludbrook's (1971) paper and made no mention of the living species, *Diastoma melanioides*. His treatment of the family placed much emphasis on sculptural characters of the protoconch and early teleoconch; moreover, he grouped genera solely on the basis of morphological similarity. I thus find his conclusions unsatisfactory. For instance, his assignment of *Bittium* to the Diastomatidae is incorrect because anatomical evidence shows that *Bittium* is closely related to *Cerithium* and falls within the Cerithiidae (see my recent remarks on this subject, Houbbrick, 1980:4–5). The *Finella* group is also more properly assigned to the Cerithiidae (Houbbrick, 1980:4), and species in the *Scaliola* group are anatomically unknown. Thus Gründel's (1976) subfamily Fenellinae is a polyphyletic group and should be excluded from the Diastomatidae.

The family name Diastomidae was correctly changed to Diastomatidae by Ludbrook (1971:31) and the latter will be used throughout this paper. Abbott (1974:107), Gründel (1976:71), and Rehder (1980:33) all incorrectly dated the family name from 1895, but Cossmann's original proposal of the family was published in 1894.

Gründel (1976:76), in a rather lengthy treatment of the Diastomatidae, concluded that the genus *Diastoma* is closely related to *Bittium*, due to similarity in shell features. His lack of acquaintance with the living species and excessive reliance on ontogenetic characters derived from protoconch and sculpture render his conclusions inadequate. Too much is known of the plasticity of developmental modes of cerithiaceans to accept protoconch shape and sculpture as conservative characters for phylogenetic speculation. Gründel's (1976:88) judgement that the presence of a well-defined anterior siphonal canal in *Bittium* species constitutes only a trivial difference ignores the functional significance of such a difference. *Bittium* species are

tiny snails that live on algae or hard substrata and represent a completely different adaptive radiation from the *Diastoma* lineage, which is adapted for burrowing in a sandy substrate.

Study of the living species, *Diastoma melanioides*, has supplied additional characters derived from the radula and anatomy which more tightly define the family limits. It is apparent that several of the small-shelled cerithiacean taxa discussed above should be excluded from the Diastomatidae and that the family as defined herein, comprises an extinct Tethyan group with a sole survivor living in south Australia. The exact status and placement of *Obtortio* and *Alaba* remain unknown until more is known of their anatomy.

Diastoma Deshayes, 1850

Diastoma Deshayes, 1850:46; 1861:411–413 (Type-species, by monotypy, *Melania costellata* Lamarck, 1804).—Tate, 1894:176–177.—Fischer, 1884:682–683.—Harris, 1897:231–232.—Cossmann, 1889:34–35; 1906:175–176.—Bartsch, 1911:581 (*non Diastoma* Deshayes).—Grant and Gale, 1931:758 (*non Diastoma* Deshayes).—Olsson, 1929:22 (*non Diastoma* Deshayes).—Wenz, 1940:749–750 (in part).—Ludbrook, 1957:22 (in part).—Pchelintsev and Korobkov, 1960:159.—Keen, 1963:32–86. (*non Diastoma* Deshayes).—Abbott, 1974:107 (*non Diastoma* Deshayes).—Emerson and Jacobson, 1976: (*non Diastoma* Deshayes).—Gründel, 1976:73–74, 76.—Houbrick, 1977:102; 1980a:3–4.—Ludbrook, 1978:112. *Neodiastoma* Cotton, 1932:541 (Type-species, by original designation, *Mesalia melanioides* Reeve, 1849).—Finlay and Marwick, 1937:42.—Marwick, 1957:162–163.—Götting, 1974:129.

Description.—Shell turreted, elongate, of moderate size with inflated whorls and ovate aperture that is broad at base and narrow posteriorly where the outer apertural lip joins the body whorl to form a sutural notch. Sculpture consists of axial ribs, thin spiral cords and occasional varices. Suture deeply incised. Columella concave with slight median, oblique fold. Anterior siphonal canal wide and shallow, not distinct from base of outer apertural lip. Outer lip of aperture thin and slightly sinuous. Operculum ovate, corneous, paucispiral, and with eccentric nucleus. Periostracum with tiny hairs. Radula taenioglossate (2 + 1 + 1 + 1 + 2). Mantle cavity deep. Ctenidium and osphradium do not extend length of mantle cavity. Salivary glands tube-like and extending through the nerve ring. Style sac and gastric shield present. Pallial gonoducts open in both sexes, males aphallate; seminal receptacle and spermatophore pouch in outer lamina of pallial oviduct. Females have a large ovipositor on right median part of mesopodium extending into center of foot and innervated by mesopodial ganglion. Nervous system epiathroid, moderately condensed with long labial and proboscis nerves and left dialyneury. Reproduction dioecious; spermatophores present; spawn and larvae unknown.

Remarks.—This genus comprises a compact group of relatively large-shelled, distinctive looking mesogastropods most of which are extinct. It is now represented by a single living species in a very restricted area along the coast of southern Australia (Fig. 6). Proposed by Deshayes in 1850, the genus is best known from the Eocene of the Paris Basin. The original generic citation in the *Atlas* of the *Traité Élémentaire de Conchyliologie* mentioned only the name, *Diastoma*. The type-species is *Melania costellata* Lamarck, 1804, by monotypy. Deshayes (1861:411) later described the genus in considerable detail from four Paris Basin species and discussed his reasons for transferring *Melania costellata* to *Diastoma*. Deshayes (1861) further remarked that *Diastoma* only superficially resembled the melanians and that the genus was closer to the Rissoidae. This has unfortunately led to confusion about the generic limits and has resulted in a polyphyletic familial concept, as discussed previously.

Tate (1894:176–177) was first to note that an Australian fossil, *Diastoma provisi* Tate, 1894, was congeneric with the living Australian snail, *Diastoma melanioides*. The latter was originally assigned by Reeve (1849) to *Mesalia* Gray, a turritellid genus. Tate (1894) noted that it superficially resembled *Mesalia*, but differed from other species in that genus by having a columellar plait, a straight outer lip, and varices. He thus transferred *Mesalia melanioides* to the genus *Diastoma*. Finlay and Marwick (1937:42) assigned *Diastoma* to the Melaniidae (=Thiaridae Troschel).

Cotton (1932:541) proposed the genus *Neodiastoma* which he assigned to the Cerithiidae to accommodate the recent species, *Diastoma melanioides*. He noted that this species differed from fossil *Diastoma costellata* by the “anterior notch of the outer lip” in the latter. Ludbrook (1971:31–32) pointed out that not all specimens of *Diastoma costellata* have the aperture separated at the suture to the same degree; thus, the presence of a sutural ramp in association with the outer lip of the anterior aperture is a variable feature. Moreover, examination of a series of Recent *Diastoma melanioides* shows that this species also has a sutural ramp at the anterior aperture although it is not as pronounced as in *Diastoma costellata*. I have figured specimens of *D. costellata* with pronounced ramps (Fig. 1E–F). A single variable shell character which is present in both fossil and Recent species does not constitute a reasonable generic character. I concur with Ludbrook (1971) that *Neodiastoma* is a synonym of *Diastoma*. Cossmann (1889:34) originally suggested that the genus was similar to *Semivertagus* Cossmann and *Fastigiella* Reeve in the placement of the median columellar fold, but I think this is more easily explained by convergence. Cossmann (1906:175) later remarked that the genus was an “ambiguous” one and noted the superficial similarity between *Diastoma* and the freshwater genus *Melania*. He did not agree with Dall’s (1889) referral of *Bittium varium* Pfeiffer to *Diastoma* and considered it a true *Bittium* species with a rudimentary canal which superficially resembled that of *Diastoma*.

Fossil record.—According to Cossmann (1906:176), this genus may date back to the Cretaceous (Senonian) but the assignment of fossils from this Period to *Diastoma*, *s.s.*, is unlikely. The genus, as defined herein, was present in the Paleocene but is best known from the Eocene and Oligocene of the Paris Basin. *Diastoma* species [Cossmann (1906) recorded 12] were widespread in the Tethys Sea. Ludbrook (1971:31) recorded the genus from Egypt, the East Indies, and North and South America, but gave no citations to support this statement. Although I have made a literature search, I have been unable to confirm the presence of *Diastoma* fossils in these areas. The genus is found in the Australian Miocene, early Pliocene, and Pleistocene where it is represented by three fossil species (Ludbrook 1971:31; 1978:112), one of which, *Diastoma melanioides*, survives to the present.

Diastoma melanioides (Reeve, 1894)

Mesalia melanioides Reeve, 1849: *Mesalia*, fig. 3, sp. 3 (Holotype: BM(NH); Type-locality, here selected: (Esperance, Western Australia).

Diastoma melanioides (Reeve), Ludbrook, 1971:32; 1978:112.

Diastoma melanoides Tate, 1894:177 (err. *pro melanioides* Reeve).

Mesalia exilis Sowerby, 1913:236, pl. 3, fig. 9 (Holotype: BM(NH); Type-locality: "West Australia."

Neodiastoma melanioides (Reeve), Cotton, 1932:541.

Synonymic remarks.—Reeve (1849) first described this species from an unknown locality and remarked that "the generic peculiarities of *Mesalia* are well represented in this species." This observation does not conform to the facts: *Mesalia* species are anatomically unknown but are thought to be members of the family Turritellidae and do not have the median columellar fold seen in *Diastoma melanioides*. Sowerby later (1913:3, 236) described the same species, naming it *Mesalia exilis*, but remarked that he was uncertain of its generic allocation. He cited West Australia as the habitat but Cotton (1932:541) noted that the type of Sowerby's *Mesalia exilis* came from Esperance Bay, Western Australia. Sowerby (1913) was either unaware of Reeve's (1849) previous description of *Mesalia melanioides* or did not regard Reeve's species to be conspecific with *Mesalia exilis*. These two taxa are, nevertheless, conspecific. Tate (1894) was the first to transfer Reeve's species from *Mesalia* to *Diastoma* and his decision was reconfirmed by Cotton (1932:541) who elected to give the living form a different generic name, *Neodiastoma*.

Ecology

Nothing has been recorded about the ecology of this species. Museum data and observations made by Mr. A. Longbottom (pers. comm.) have supplied the sparse information presented below. *Diastoma melanioides* lives subtidally in depths of 1–5 meters where it burrows in clean white sand



Fig. 6. Geographic distribution of *Diastoma melanioides* based on museum specimens and records cited by Ludbrook (1957). Star represents a fossil from the Ecula Basin.

associated with grass beds and algae. Its presence may be detected by long trails in the sand. The large gastric shield and style sac indicate an herbivorous mode of feeding; moreover, the tiny jaws, small taenioglossate radula, stomach contents, and fecal pellets comprised of fine sand grains and detritus suggest that *Diastoma* feeds on microalgae and detrital particles found in the sandy substrate. Repaired shells indicated that this species is attacked by crabs. Although no drilled shells were seen, the sandy habitat also suggests possible predation by naticid snails. Paired snails were collected in June (Longbottom, pers. comm.) and large ova were found in the ovaries of preserved animals collected in July. This may indicate an early winter breeding season. The spawn is undescribed, but the presence of a large ovipositor and associated mucoid-jelly gland suggests a jelly-like spawn

mass not unlike those described for other cerithiacean snails. The bulbous, smooth protoconchs and restricted distribution are indicative of direct development.

Ludbrook (1971:30) presented a map showing the summer isotherms of the Great Australian Bight. These indicate that *Diastoma* lives well within the warm temperature 19–20°C isotherms.

Conclusions

The shell and anatomy of *Diastoma melanioides* establish beyond doubt that it is the superfamily Cerithiacea. Features common to the superfamily are the open pallial gonoducts, aphyallic males, and general layout of the alimentary tract which includes a taenioglossate radula, paired salivary glands and stomach with a style sac, gastric shield, and reduced spiral caecum.

Distinctive features which establish the familial status of the group are the elongate shell with its wide aperture, indistinct inhalant siphonal canal, and deeply impressed suture and ramp. The shell shape is much like those of the freshwater melanians. The thick, slightly hairy periostracum is an unusual trait for a burrowing snail. I know of no other cerithiacean having a similar periostracum although *Campanile symbolicum*, which is sympatric with *Diastoma*, has a strange calcified periostracum (Houbrick, 1981a).

The anatomy of *Diastoma* differs markedly from other cerithiaceans by a number of diagnostic features:

- 1) The highly extensible snout and large cephalic cavity are notable characters. The snout of *Diastoma* is wider and longer in relation to body size than in most cerithiaceans but there is some resemblance to burrowing, sand-dwelling cerithiid snails such as *Rhinoclavis fasciata* (Bruguere), *R. vertagus* (Linnaeus) and *R. aspera* (Linnaeus) (Houbrick, 1978). The relatively small buccal mass, jaws, and generalized taenioglossate radula are not diagnostic at the familial level.

- 2) The paired worm-like salivary glands extend through the nerve ring, are unusually long and simple, and constitute a distinctive character. In contrast to *Diastoma*, the salivary glands of all observed cerithiid and modiolid snails are spongy masses of tissue having long, thin ducts and, with the exception of a small part of the left salivary gland, lie anterior to the nerve ring (Houbrick, 1980:124). Some members of the Potamididae, such as *Cerithidea scalariformis* (Say) and *Batillaria minima* (Gmelin) have more simple, worm-like salivary glands like *Diastoma* but the greater part of these glands lies well anterior to the nerve ring (personal observation).

- 3) An unusual feature of the anterior and mid-esophagus of *Diastoma* is its loose connection to the walls of the spacious cephalic cavity by numerous, long muscular strands. The muscles are inserted on the esophagus

where it passes through the nerve ring and are also loosely connected to the ganglia. The esophagus is thus able to move somewhat through the nerve ring when the snout is extended. I have not seen this kind of anatomical flexibility in the anterior esophagus of any other cerithiacean.

4) The pallial gonoduct of *Diastoma* has a simple, generalized arrangement. The spermatophore pouch and seminal receptacle are located in the outer lamina of the pallial oviduct and comprise a simple, bifurcate chamber. Other cerithiaceans, such as the cerithiids, modulids, melanians, and turritellids, while having a similar ground plan to the pallial oviduct, display greater complexity in the internal structures associated with the seminal receptacle, spermatophore pouch and sperm collecting gutters.

5) An unusual diagnostic character of *Diastoma* is the large, complex ovipositor which is found on the mesopodium of females. Although ovipositors have been noted in other marine cerithiacean snails such as *Cerithium* (Marcus and Marcus, 1964:500) and *Modulus* (Houbrick, 1980b:121), I know of no other marine snail in which there is a large mucus-producing gland located within the center of the mesopodium and connected to the external ovipositor. It is assumed that this gland contributes to the formation of the egg mass, which is probably very gelatinous. Belgin (1973:390, fig. 7) has shown a very similar ovipositor in *Zemelanopsis*, a freshwater melanian snail, but gave no details about its internal structure other than to say that it was a deep pit bordered by a muscular lobe.

6) A diagnostic feature of the nervous system of *Diastoma* is the length of the labial and buccal nerves and the innervation of the ovipositor organ by the mesopodial ganglion and its ancessory nerves. The nervous system is moderately concentrated having an RPG ratio which lies between the values observed in members of the Cerithiidae and Potamididae.

7) In *Diastoma*, the proximal ends of the osphradium, ctenidium, and hypobranchial gland are not located at the posterior end of the mantle cavity. Instead they begin anterior to it, which is an unusual feature. In members of the Cerithiidae, Potamididae, Modulidae, and Turritellidae, these organs extend the length of the mantle cavity, but in freshwater melanian species of *Zemelanopsis* they appear to be shortened as in *Diastoma* (Belgin, 1973:390, fig. 7).

While taxonomic criteria for the familial status of a group are ill-defined and somewhat arbitrary, I believe that the characters derived from the shell and anatomy of *Diastoma* are of sufficient diagnostic weight to establish the group as a distinct family. To these I add the additional evidence of a long fossil record which shows that these species comprised a distinct group since the early Tertiary. It may be argued that the overall resemblance of *Diastoma* to the cerithiids is quite close and that the evidence for familial status is not convincing. Nevertheless, the observed differences indicate to me a higher taxonomic category for the group than a generic one.

The shell and anatomy of *Diastoma* are most like those observed in members of the Cerithiidae and Potamididae and very much like those of some species of the freshwater family Melanopsidae H. and A. Adams. It is possible that *Diastoma* is the marine branch of that family, but not enough comparative material has been analyzed to say more on this subject. Although this resemblance may be due to convergence, it is likely that the Diastomatidae are closely related to these cerithiacean families. The shell of *Diastoma*, in contrast to those of members of the above-mentioned families, lacks a distinct anterior canal and its aperture is more like those seen in smaller-shelled members of the Dialidae. There may be a relationship between these two groups but nothing is now known of the anatomy of *Diala*.

The relationship between *Diastoma melanioides* and the Australian fossil *Diastoma* species is clearly a close one (Ludbrook, 1971:131). There is no way to demonstrate with certainty that this Australian assemblage belongs to the same lineage as the Tethyan group of European fossils which bears the same generic name. As is so often the case, the type-species of the genus, *Diastoma costellata*, is rather atypical of the group. The axial ribs are more pronounced and the sutural ramp, formed where the outer lip meets the body whorl, is more exaggerated than in most *Diastoma* species (see illustrations in Fig. 1E–F). Examination of a number of specimens of this species shows that this character varies in intensity and is most pronounced in older specimens. Moreover, other Tethyan *Diastoma* species do not have this feature in so pronounced a state. It should also be noted that a similar, but weaker sutural ramp is present in the living species and was figured by Ludbrook (1971:fig. 13).

The main conchological difference between the Australian and European fossils is the presence of the median columellar fold in species of the former. This fold does not extend up the shell axis but appears to be merely a thickening of the columellar callus. Cotton (1932), noting this difference between the living species and the European fossils, considered it to be of generic significance. I do not believe a simple character should be so heavily weighted. Although the two assemblages may constitute different generic taxa, I regard them as being of the same lineage and prefer to retain all species with the genus *Diastoma* until more detailed analysis of the fossil species is made.

Members of the Diastomatidae probably lived throughout the Tethys Sea during the Tertiary. Other Tethyan survivors are found in the Australian region and include prosobranchs such as *Campanile symbolicum* Iredale (Houbrick, 1981a), *Gourmya gourmyi* (Crosse) (Houbrick, 1981b), and the bivalve genus *Neotrigonia*, family Trigoniidae, which became largely extinct in the Cretaceous. These relict species probably remained in the Australian area after the closure of the Tethys in the Miocene.

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